The Biology and Population Ecology of Two Species of *Cardiaspina* (Hemiptera: Psyllidae) in Plague Numbers on *Eucalyptus grandis* in New South Wales

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The genus *Cardiaspina* contains at least five species whose populations increase to very high numbers from time to time. Three species investigated have all caused severe defoliation of prized economic forest tree species of *Eucalyptus*. Historic occurrences are recorded as far as possible but it is probable that such outbreaks also happened long before man's intervention in Australian forests.

In this paper the two species *Cardiaspina fiscella* Taylor and *Cardiaspina maniformis* Taylor have been studied in some detail as they have a common host in the tree *Eucalyptus grandis* Hill & Maiden (the rose or flooded gum) and because of their peculiar and unusual behaviour. Their biology and population ecology is examined and the influence of various biological factors on fluctuations in their numbers discussed. Various aspects of tree and leaf conditions and the possible effects of weather on their populations are also considered. An hypothesis of psyllid outbreak release is presented for consideration.

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INTRODUCTION

There are many species of *Cardiaspina* having *Eucalyptus* spp. as hosts but so far only five species are known to have caused significant or widespread defoliation of trees in south-eastern Australia.

The earliest record of *Cardiaspina* species causing widespread defoliation in New South Wales was in the summer of 1910 in the then Forestry District of Taree (Forestry Commission of N.S.W., unpublished data). Stands of *Eucalyptus paniculata* Smith (grey ironbark) were reported as being severely defoliated. In March 1916 the insects responsible were reported as still infesting the trees and increasing in number; in May W. W. Froggatt visited the area and later described the insect responsible as *C. vittaformis* (Froggatt, 1923). The outbreaks continued until 1936.

High numbers of *C. albitextura* Taylor occurring on *E. blakelyi* Maiden (red gum) in the Australian Capital Territory and Southern Tablelands and south-west slopes of eastern Australia have been studied in detail by Clark (1962, 1963 a, b, c, d, 1964 a, b, c) these papers provided an excellent and comprehensive study of the population ecology of this insect.

C. densitexta Taylor, which occurred in epidemic numbers on *Eucalyptus fasciculosa* F. Muell in parts of South Australia from 1914-22 and also in 1956-63, has been intensively studied by White (1966, 1968a, b, 1969, 1970). These papers dealt with many aspects of the biology and population ecology of this insect/tree relationship and provided a comprehensive understanding of this complex interaction.

In 1938 a species of *Cardiaspina* was found to be defoliating *E. botryoides* Smith (bangalay) at Narrabeen (Sydney, New South Wales). This and another *Cardiaspina* species were defoliating *Eucalyptus grandis* Hill & Maiden (rose or flooded gum) in the Boambee-Coffs Harbour area in the 1960's and these outbreaks have occurred sporadically since. In 1961 defoliation of *E. grandis* in the Boambee area was severe and a study of the outbreak was commenced by the author in the same year. The two species involved were *Cardiaspina maniformis* and *C. fiscella* and were described and named by Taylor (1962). This paper gives an account of the biology and behaviour of these two insects, various controlling factors and some of their population dynamics. Records of past plagues of *Cardiaspina vittaformis* are also included; the life history of this species was described by Froggatt (1923).

Plague Records

Cardiaspina vittaformis *Froggatt*

Infestations of this insect were first reported (Forestry Commission of N.S.W., 1910, unpublished data) in the southern part of the then Taree Forestry District near Dungog and Clarencetown on ironbarks (mainly *E. paniculata* Smith). In the Caincross and Kiwarrak State Forests trees were severely defoliated and outbreaks extended as far north as the Hastings River. It was reported that the ironbarks usually recovered from initial defoliation, but repeated attacks caused a great amount of 'die-back' of the crowns and a number of trees died. Outbreaks continued during 1917-18, and in 1919 the insect was in very high numbers in the northern part of the district in the Maria River, Tanban and Yessabah State Forests (Kempsey Forestry District). In 1920 it was reported only from Trevor State Forest and Froggatt (1923) mentioned it as present but not doing much damage.

In 1924-25 the psyllid was again present in high numbers, this time in Ingalba and Collombatti State Forests; it gradually extended northwards in 1926-27. Saplings and pole-sized trees were killed. The insect was less active in the Taree District but did considerable damage in the Kempsey District. In 1928-34 defoliation caused by *C. vittaformis* was severe in Kiwarrak, Broken Bay, Caincross and Bullengarra State Forests. In the Taree and Wauchope Districts, the heaviest damage occurred between 1924-30, only scattered attacks being noted in 1932-33. The insect was present in high numbers again on *E. paniculata* in 1936 in Olney State Forest between Martinsdale and Olney plantation as well as in the Taree and Wauchope Districts at Broken Bay, Bull's Ground, Keri, Lorne, and Cowarra State Forests; however, the outbreaks were brief and numbers diminished again within the year.

Large numbers of ironbarks were felled and logged as a result of the 1916-30 outbreaks, the practice being to mark for felling and removal trees with their larger branches dead. In almost all cases the upper part of the main trunk of the trees felled (0.6-0.9 m down) showed heart 'doze' (decay due to wood-rotting fungus). This is most unusual in ironbark and was attributed to the psyllid attack killing major parts of the crown and permitting fungal infection of the large branches and the upper trunk.

The remnant ironbark stands at Beecroft and West Pennant Hills (New South Wales) were severely defoliated by *C. vittaformis* in the 1960-64 period but no outbreaks occurred in the areas previously affected in the lower north coast. Another ironbark, *Eucalyptus siderophloia* Benth., was hardly affected by this psyllid.

Cardiaspina fiscella

Although no doubt occurring in high numbers earlier, *C. fiscella* was first reported to cause defoliation, of *Eucalyptus botryoides* Smith (bangalay) at Narrabeen and on the closely related *Eucalyptus grandis* (near Coff's Harbour), in 1938. In 1944 the outbreaks were widespread and *Eucalyptus saligna* Smith (Sydney blue gum) was also reported as being defoliated at Barengarry Mountain and between Bulli and Nowra as well as in the Kangaroo Valley.

This species also defoliated *E. grandis* around Coff's Harbour, especially in Mooball State Forest on the lower slopes of the southern approach to the Burringar Range. Lighter attacks occurred further north in the Tweed area. *E. botryoides* at Narrabeen and around the foreshores of Port Jackson was also attacked in 1944. Outbreaks continued throughout 1945-47 in the Coff's Harbour, Bonville, Korora and Boambee State Forests and near the Pine Creek State Forest nursery; other infestations occurred between Murwillumbah and Mullumbimby.

In Boambee State Forest natural regeneration was severely defoliated, but planted trees were only slightly affected. Some defoliation of the bangalay occurred at Collaroy in 1946. No further outbreaks were recorded until 1954 when *E. botryoides* at Narrabeen and the Royal National Park were defoliated.

In 1957 *E. grandis* at Korora was defoliated and this continued in 1958. In 1959 *Eucalyptus botryoides* at Gosford was attacked. Early in 1961 defoliation of flooded gum was severe in compartments 101 and 102 of the Boambee State Forest and was widespread, extending from South Boambee in a roughly east-west line through South Korora to Mt. Brown, south of Karangi. However, the insects were not present in high numbers in any of the areas of Pine Creek (Whian Whian) State Forest affected in 1946 or further south. In 1948 the *E. grandis* plantations in Whian Whian State Forest were defoliated (Taylor, 1990, pers. comm.), the '80 acre', was severely defoliated — *C. maniformis* was also present. In compartment 16 the insects were present but defoliation was not severe. In No. 1 and Seaview only light defoliation was noted. The natural regeneration of *E. grandis* west of the nursery was the most severely affected.

A detailed study of this latter series of outbreaks in the Boambee area was commenced and it was soon established that two species of *Cardiaspina* were involved. *C. maniformis* was, no doubt, present in all the earlier recorded outbreaks on the lower north coast, but it was not described or named by Taylor until 1962.

LIFE HISTORIES AND BEHAVIOUR

Cardiaspina maniformis

This psyllid occurs on *Eucalyptus grandis* in association with *C. fiscella*. Very often both species are present in the same leaf; the leaves of *E. grandis* are dorsiventral and the dorsal surface of the leaf has few stomatal apertures, most being on the ventral surface.

The eggs are deposited on the dorsal surface of the leaf. After eclosion, the nymph establishes itself, also on the dorsal surface, begins to feed and constructs its covering or 'lerp'. There are five nymphal instars (Fig. 1**a**) and after each moult the perimeter of the lerp is increased to accommodate the insect's greater bulk. Eventually the shell-like lerp characteristic of the species is attained at full growth (Taylor, 1962). The nymphs may be parasitized by small endoparasitic or hyperparasitic wasps. In this case a black nymphal 'mummy', instead of a healthy full-grown nymph results.

After emergence and copulation, the female actively seeks oviposition sites, although adult feeding does not cause significant damage to the leaves as the insect seldom remains in any spot for any time. It is probable that this is the way she also determines whether a leaf is suitable for oviposition and probably as a feeding site for a nymph. Males and females are winged and very mobile, jumping away backwards if threatened. Tender new leaves are not favoured for oviposition, nor are the dead or dried portions damaged by former nymphal feeding; mature and healthy leaves are chosen where possible. Intensive investigation of the mating and oviposition behaviour of *C.*

densitexta on *E. fasciculosa* has shown that the nature and condition of the leaves is critical (White, 1970).

The eggs are a little larger than a first instar nymph and are laid singly but usually adjacent to one another. They are affixed to the leaf surface by a small stalk (illustrated in Froggatt, 1923). *C. maniformis* has four generations a year; all of these may overlap to some extent as indicated in Fig. 1a.

Cardiaspina fiscella

Soon after emergence the adults of this psyllid oviposit on either surface of the *Eucalyptus* leaf, but more frequently on the dorsal surface — often at sites adjoining those of *C. maniformis*. However, the first instar nymph practically always establishes its feeding position on the ventral side of the leaf, as they are capable of walking from a crowded or unsuitable site to one more favourable. If they do not find a suitable site within a few hours they will die from exhaustion. Later instars appear incapable of changing their feeding positions. There are five nymphal instars (Fig. **1b**) and at each moult the insect adds to its lerp covering until, at the last instar, the lerp attains its characteristic shape (Taylor, 1962).

Oviposition

The presence of two species of insects of the same genus on the same host would seem to pose a paradox. However, the obvious ability of these two species to coexist on the same leaf of the host plant, even at very high population densities is seemingly explained by their nymphal behaviour.

Although eggs are laid by *C. maniformis* only on the dorsal leaf surface, those of *C. fiscella* are laid on either surface but it also prefers the dorsal surface. However, when the nymphs eclode, those of *C. maniformis* almost invariably choose feeding sites on the dorsal surface, but *C. fiscella* nymphs seek theirs on the ventral surface.

Selection of Nymph Feeding Sites

In order to determine why nymphs of each species choose their respective feeding sites on the same leaf, a number of leaves with eggs of both species were artificially inverted and held in this position while still living and affixed to their twigs on the tree. Thus the ventral surfaces of the dorsiventral leaves faced upwards and toward the sun and the dorsal surfaces faced downward toward the ground. All the leaves chosen were wholesome and good feeding sites.

After eclosion in every instance the *C. maniformis* nymphs established themselves on the now downward facing dorsal surfaces and *C. fiscella* on the upward facing ventral surfaces, precisely as they would if the leaves were oriented naturally. Many of the nymphs successfully completed their stages. Their behaviour seemed to be neither geotactic or phototactic.

Microscopic examination of nymphs in place on leaves revealed that the stylets of *C. maniformis* readily penetrate the dorsal cuticle. However, *C. fiscella* seems to be unable to achieve this and the nymphal stylets of this insect penetrated through the stomatal apertures, which are mainly on the ventral surfaces of leaves. White (1970) recorded that *C. densitexta* nymphs also fed through the stomates of *E. fasciculosa*. When *C. fiscella* nymphs were gently removed from their feeding sites they had great difficulty in re-establishing themselves, whereas *C. maniformis* did so without much trouble.

As feeding destroys leaf tissue and a well established nymph does not move from its site (not even when attacked by a ferocious syrphid larva), necrotic patches on the leaf surface slowly enlarge. If these patches overlap some interspecific and intraspecific competition does occur, but it is usually only when the insect population is dense that

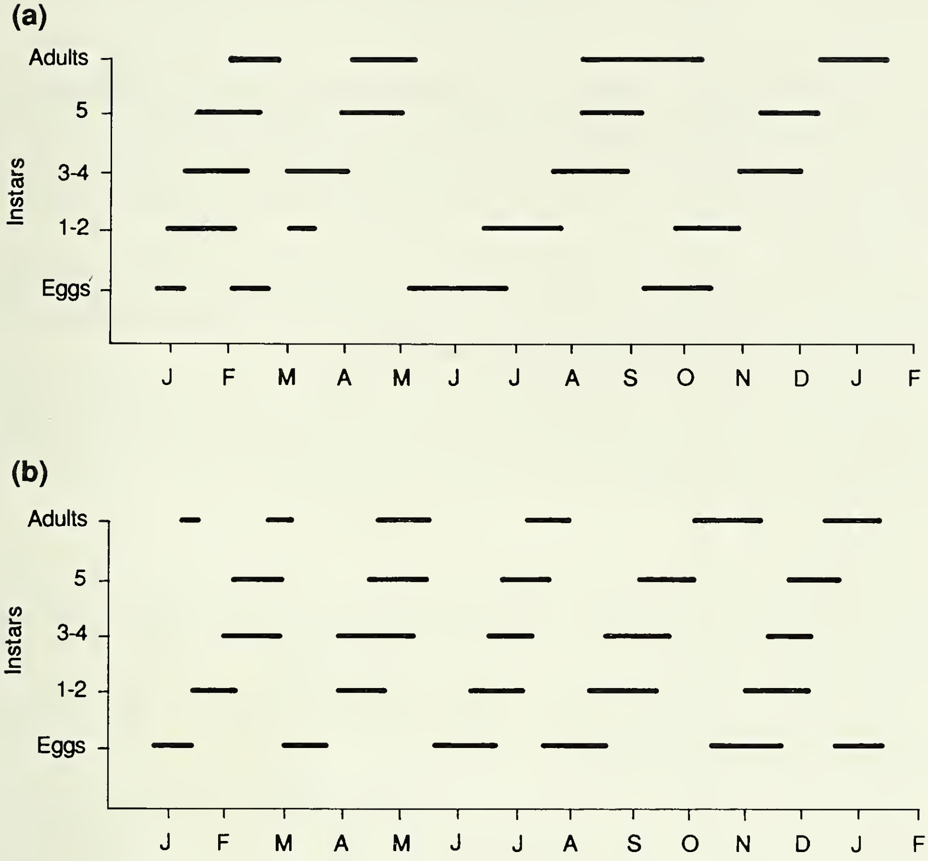

Fig. 1. Occurrence of psyllid life cycle stages over a 15 month period: (a) *Cardiaspina maniformis*; (b) *C. fiscella*.

nymphal mortality follows. If damage is too great the leaf is shed by the host tree. At the end of a nymphal stage damage to leaves can be so great even at reasonably low population densities that severe defoliation can ensue. The consequences of this will be discussed later (see also Clark, 1963a). Clark (1963b) gave a good account of the behaviour of *C. albitextura* on *E. blakelyi*. White (1970) provided comprehensive descriptions of behaviour patterns in adults of *C. densitexta*.

The males of each species produce distinctive calls, different for each species and are probably used to attract appropriate females (Campbell, 1964). This ability may be critical when numbers are low and the finding of suitable mates important. A comparison of the sounds produced by *C. maniformis*, *C. fiscella* and *C. densitexta* would be informative.

Mortality Factors

A number of mortality factors which affect psyllid numbers are considered below. These include: endoparasitic wasps; predatory insects; predatory birds; foliage and tree conditions.

Endoparasities

The larvae of several species of *Psyllaephagus* Riek and *Quaylea* (Hymenoptera: Encyrtidae) are parasitic on psyllid nymphs. Species recorded include: *P. gemitus*, *P. cornuatus*, *P. bliteus*, *P. discretus*, *P. facilis*, *P. funiculus*, *P. brachiatus* and *P.* nr *dignus* and *P. clarus* (Riek, 1962, 1970). At Boambee, three species were most prevalent, *P. gemitus* Riek, *P. clarus* Riek and *Q. psyllae*. The relative abundances of these from 1961-63 is shown in Fig. 2.

Numbers of the primary parasite, *P. gemitus*, were low and insignificant compared to those of the hyperparasites during the periods of high psyllid numbers in 1961-62. This suggests that comparative failure of the primary parasite contributed to favourable conditions for psyllid population outbreak (see Fig. 3)

A parasitized nymph does not emerge as an adult but is eaten inside its case by the wasp larva; a black 'mummy' results from which the adult wasp emerges. These can be readily detected on close examination during a census (Clark, 1964a). Many parasitoids are attacked by hyperparasites; this does not alter the mortality as far as the psyllids are concerned but may alter the longer term effects of parasitizm.

Predators

Larvae of the hover fly, *Syrphus viridiceps*, (Diptera: Syrphidae) are voracious predators of nymphs (Fig. 3), though less during winter; however, they are relatively rare and their total effect is uncertain — see Clark (1963d, 1964a). An occasional lacewing (Neuroptera) larva was observed to predate on psyllid nymphs.

Some small birds, such as the weebill (*Smicornis brevirostris*) and the pardalotes (*Pardalotus* spp.) were observed feeding on the nymphs. No doubt these birds also feed on adult psyllids (see Clark, 1964b).

The effect of insectivorous birds on any insect population is very complex, as the bird is just as likely to eat parasites or predators of the insect as the insect itself (Campbell and Moore, 1957; Ward and Neumann, 1982). There is the possibility that this may increase survival rather than mortality of the psyllids and actually increase population numbers, as has been observed in the case of the plague phasmatids (Readshaw, 1964). The actual effect of birds on psyllid numbers requires further study (Ward and Neumann, 1982).

Host Conditions/Interactions

All recorded outbreaks of these psyllids have occurred in areas of good 'site quality' (S.Q.). This is a forestry estimate of the total effect of all growth factors of a particular site on tree growth and health: S.Q.1 is very good, whereas S.Q.7 is extremely poor. The trees considered in these studies were mostly over five years old and not far from the sea. The favoured condition of leaves for oviposition by the psyllid adults has already been stated.

Feeding by the nymphs (sucking the sap from a leaf) ultimately results in a small portion of the leaf being killed. The initial amount of a leaf's tissue killed depends on the number of nymphs feeding in one generation. If numbers are low and only a small amount of tissue is necrotic, reinfestation of that leaf may occur and the feeding and necrosis will continue and spread. When this damage reaches a point where the leaf requires more energy to maintain it than it is returning to the tree, by photosynthesis, it

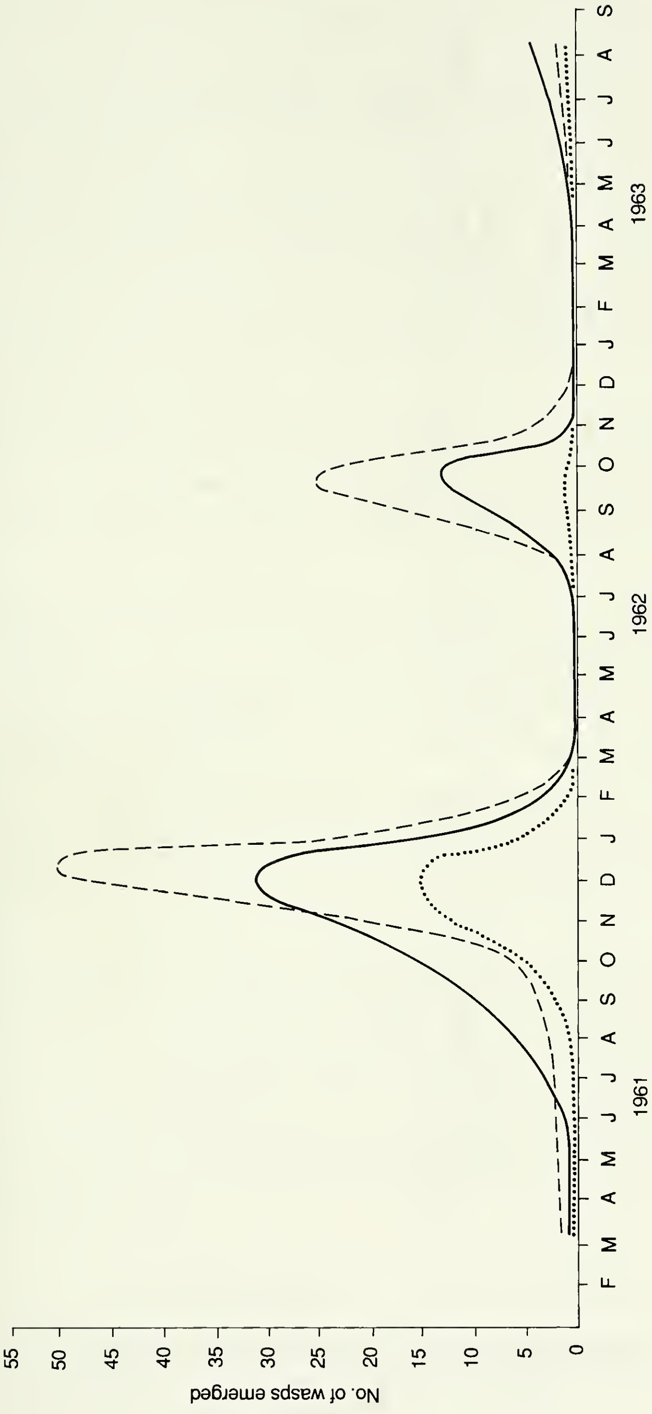

Fig. 2. Relative abundances of 3 parasitic wasps that emerge from 'mummies' of *C. maniformis* and *C. fiscella*; *Psyllaephagus gemitus* (——), *P. clarus* (– – –), *Quaylea psyllae* (.…).

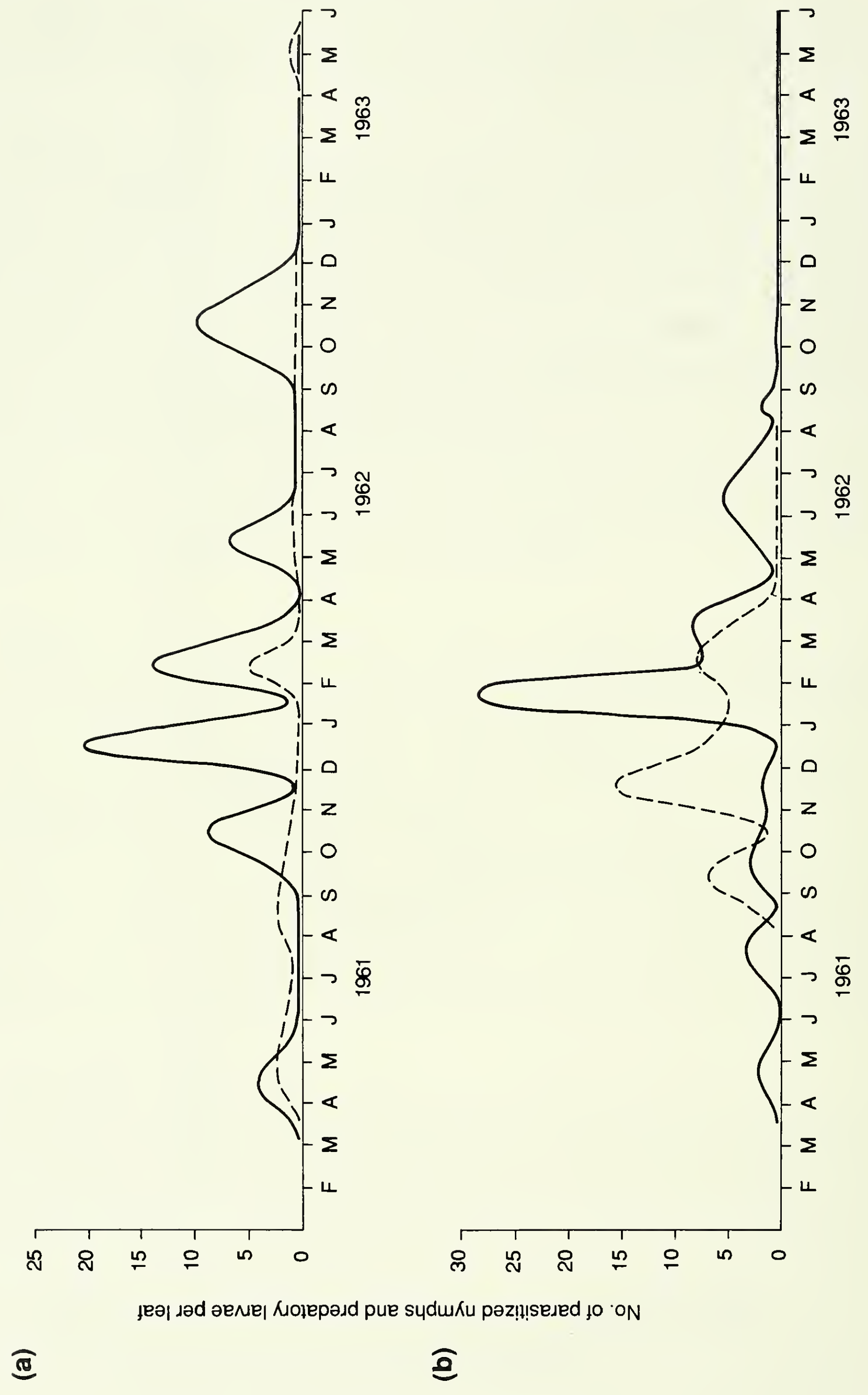

Fig. 3. Parasitizm and predation of *Cardiaspina fiscella* and *C. maniformis*; parasitized nymphs (——), predatory larvae (----). (a) Boambee Plantation, (b) South Boambee (6 *C. fiscella*: 1 *C. maniformis*).

is shed and all the nymphs feeding on it, unless they are fully fed and ready to metamorphose, perish.

Leaves are also shed, although they may be still functional, if they become redundant to the tree; this happens when a 'flush' of growth occurs in eucalypts as a result of good growing conditions. This type of leaf loss can also be disastrous to eggs or nymphs present on such leaves.

When population numbers of psyllids increase to the extent that most or all the leaves reach this critical damaged condition at much the same time then a large part of the foliage will be shed, sometimes over quite a large area of forest. This causes a short-term setback for the trees as stored reserves must be channelled immediately into leaf production instead of into progressive growth, normal leaf replacement or wound repair. For a vigorous tree like *E. grandis* growing on a good site this is not a disaster, although it could be to trees growing on poorer sites with less stored reserves (cf. *E. paniculata*, *E. blakelyi*, and *E. fasciculosa*).

The shedding of foliage usually causes a reduction in growth, particularly in wood production; this is of serious concern for forest managers. Prolonged plague numbers can virtually stop tree growth for several years as the tree puts all its energy into maintenance and replacement. Trees can actually be reduced in diameter if all the foliage is damaged (Mazanec, 1966). Also, a tree weakened in this way is subject to 'die-back'.

For high numbers of psyllids to be maintained an ample supply of good oviposition sites in the first case and enough good leaf tissue for nymphal establishment, feeding and survival to full growth is necessary. In the initial stage of a population increase these conditions are abundant and the adults can lay their full quota of eggs. Most of these will survive as will the ecloding nymphs and an explosion in numbers results. If the trees can maintain an adequate supply of suitable leaves to meet this increase in the psyllids, plague conditions will be maintained.

This situation can change quite rapidly if the defoliation of the trees outstrips their ability to refoliate. New and immature leaves are not favoured oviposition sites or feeding sites for the nymphs, so that the psyllid population can then diminish as quickly as it has increased (see Fig. 4). Recovery can occur when the foliage conditions become favourable again.

In the case of *E. grandis* which is very vigorous, probably the fastest growing of all the *Eucalyptus* species, a tree can cope with high psyllid numbers for quite some time. Repeated defoliation, however, will ultimately use up its energy and stored reserves more rapidly than they can be replaced by photosynthesis. The increase in psyllid numbers is thus closely related to the ability of the host tree to sustain the insect population. Thus, it is possible for a host tree to 'regulate' a psyllid plague either by not maintaining enough suitable foliage or by producing too much (new and immature) foliage which is unsuitable. A similar interaction between insect and host has been noted with *C. albitextura* and *E. blakelyi* (Clark, 1963a,b), as well as *C. densitexta* and *E. fasciculosa* (White, 1966, 1970).

POPULATION STUDIES

Sites and Samples

From early 1961 to mid 1963 a census of the psyllid populations was taken each month at five different sites. These are listed and described below.

1) Inside Boambee State Forest Plantation — in an area previously seriously defoliated.
2) Inside the Boambee Plantation — in an area only moderately defoliated previously.

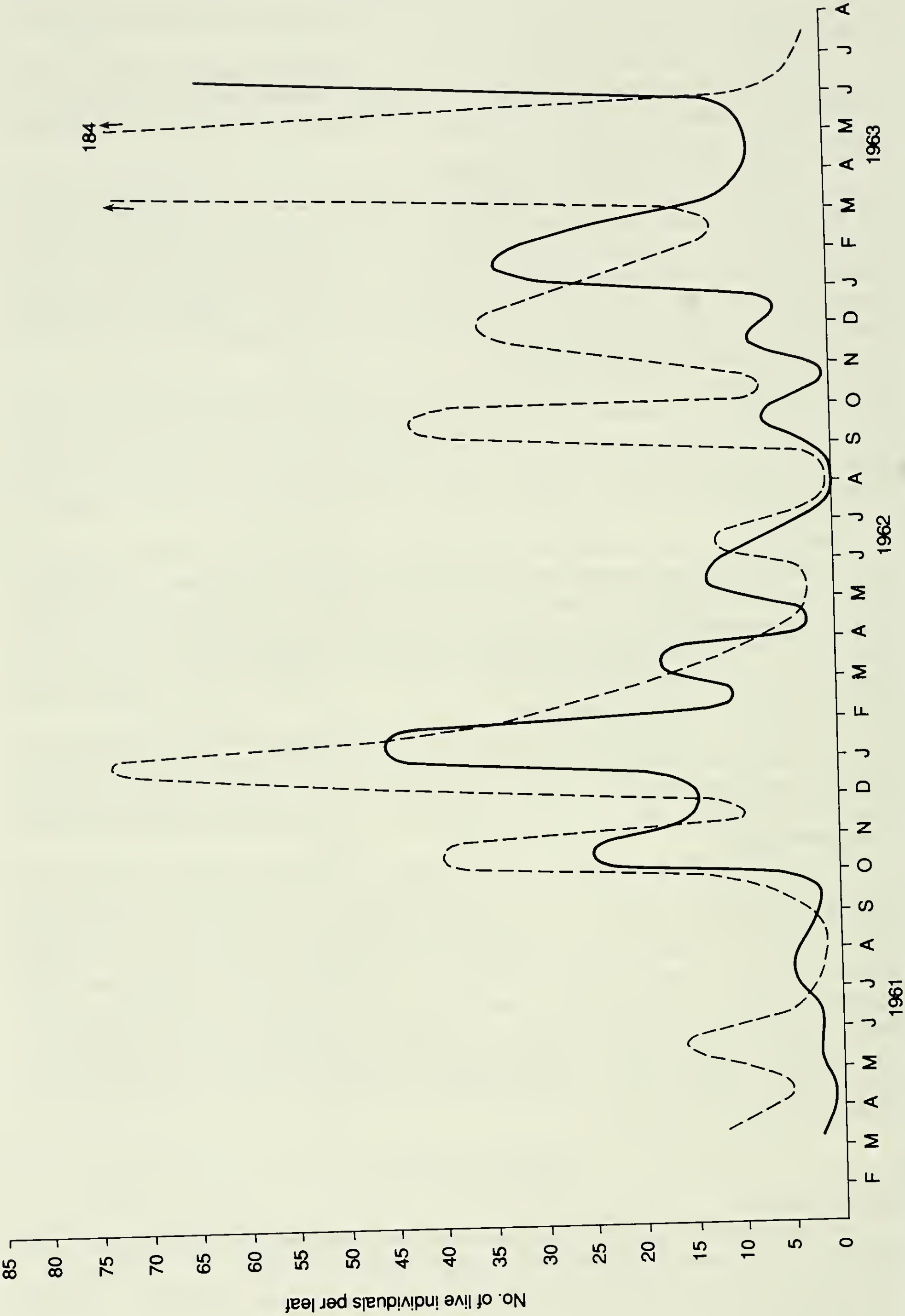

Fig. 4. Population trends of psyllids at South Boambee; *Cardiaspina fiscella* predominates, 6:1. Eggs (----); nymphs (——).

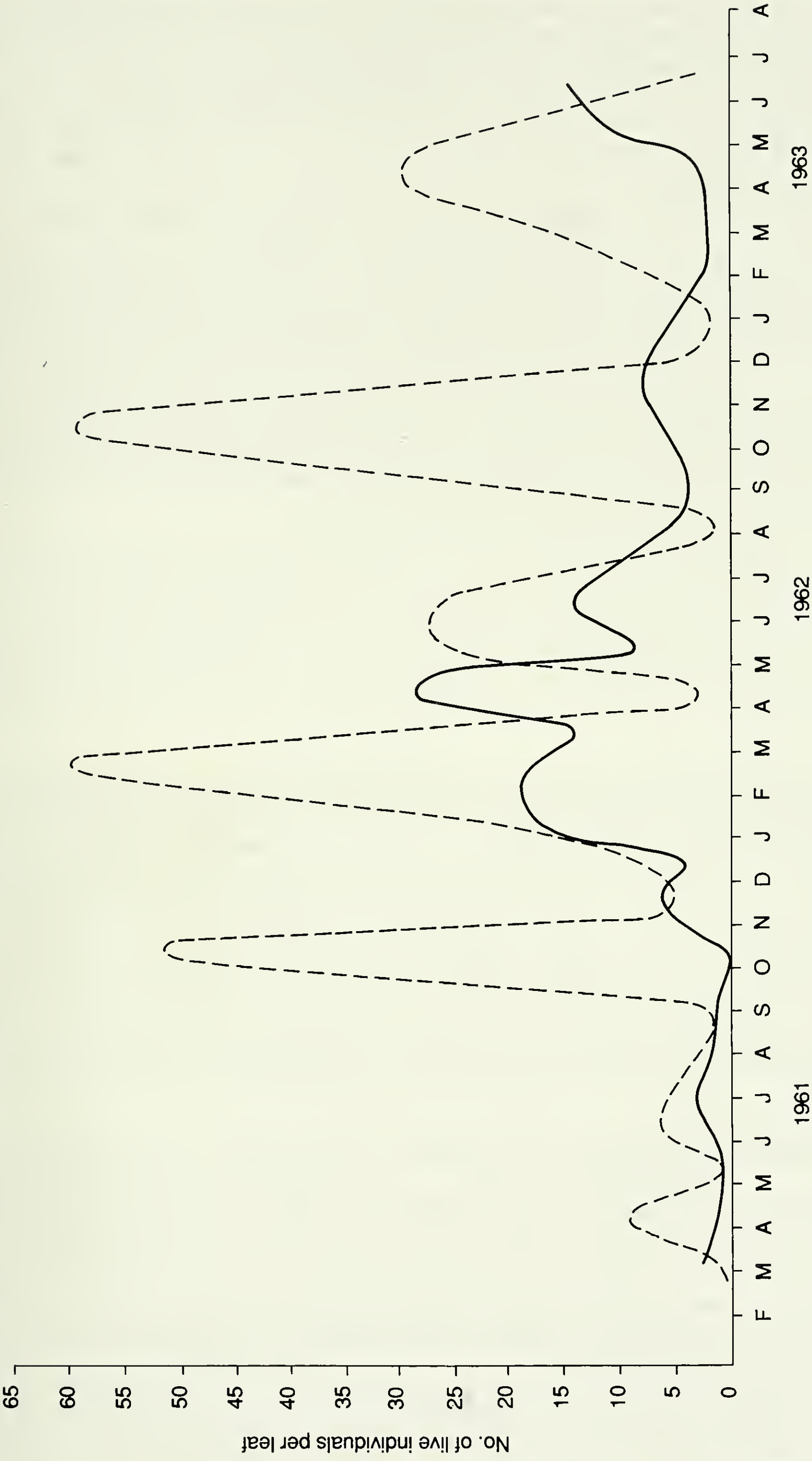

Fig. 5. Population trends of *Cardiaspina maniformis* at Boambee Plantation. Eggs (----), nymphs (——).

At 1) and 2) two trees were sampled on each occasion. Five branchlets approximately 23 centimetres long (10 leaves) were taken from (a) the top, (b) the middle and (c) the bottom of the crown (i.e. 15 branchlets from each tree).

3) Outside Boambee Plantation — open grown natural regeneration on private property.
4) Middle Boambee, as in 3).
5) South Boambee.

At 3), 4) and 5), 10 branchlets each of 10 leaves were taken at random from one tree at each site (reduced to 5 branchlets each after 5 June, 1962).

From each leaf, counts of eggs, nymphs — live and dead (lerps without live nymphs) and parasitized nymphs were made; *C. maniformis* and *C. fiscella* were recorded separately. Each psyllid species has a quite characteristic and easily recognized lerp (Taylor, 1962). Counts of numbers of predators and observations and notes of host leaf conditions were also made. Thus the numbers per leaf given in the figures are an average of 150 leaves per tree on sites 1 and 2 and 100 (later 50) leaves at sites 3, 4 and 5.

Figs 2 to 6 illustrate population trends in two different localities. The biotic mortality factors (wasp endoparasites and predators) are shown in Figs 2 and 3; Figs 4, 5 and 6 demonstrate the variation in psyllid populations.

C. maniformis was predominant in the Boambee State Forest Plantation, where the trees are artificially regenerated and the trunks close together with dense tight crowns; both species were present, often on the same leaf. *C. fiscella* predominated in the more open crowned, naturally regenerated area at South Boambee. Again both species were present (often on the same leaf) in the ratio of 6 *C.f*: 1 *C.m*). Despite this the fluctuations in numbers of the various life stages and generations of both insects at each site were synchronized.

Cardiaspina maniformis

In the case of *C. maniformis* in Boambee State Forest Plantation the foliage was not so badly damaged in 1961 and few new leaves were produced by the host in March. Numbers of psyllid nymphs reached their peak numbers in April, 1962, but at a much lower level than those of *C. fiscella* had at South Boambee earlier in January (Figs 5 and 6). Damage to the leaves was not then severe and these leaves were retained by the trees well into 1963.

Parasitizm was also generally higher in nymphs of *C. maniformis* and the tiny wasps were active to the end of 1962, but few were in evidence in 1963, when numbers of psyllids again began to increase (Fig. 3). The syrphid larvae also appeared less active in the plantation area. In 1964 the population of both psyllid species fell to very low numbers.

Cardiaspina fiscella

In the fourth generation of 1961 and first generation of 1962 the feeding of high numbers of nymphs of the *C. fiscella* dominated population caused severe damage to leaves of the host trees. Although new leaves were beginning to be produced, refoliation was not complete until about September 1962, when another build-up to high numbers culminated in the second and third generation in 1963 (Fig. 4). Parasites and predators were common and no doubt helped to reduce numbers in 1962; but after August 1962 they were less significant and psyllid numbers again began to increase to the very high levels recorded in mid 1963.

Predation effects were difficult to assess; the main predators were syrphid fly larvae, some neuropterans and birds. No doubt a syrphid larva eats many psyllid nymphs during its lifetime but it is also readily taken by insectivorous birds (Campbell and Moore, 1957). For example, in January 1962, of 77 lerps on a leaf (1st and 3rd instar) 31 had the nymph removed and in February 1962, of 97 lerps, 87 lerps had the nymph removed. The lerps were undamaged and the only predators present capable of removing the small nymph without doing this were the syrphid larvae, of which there were quite a number present. Birds damage the lerp considerably when seeking the nymph beneath; see Clark (1964b) for the effects of syrphids and birds on *C. albitextura.*

In the Sydney area *C. fiscella* was in high numbers on *E. botryoides* (bangalay) on the northern shore of Narrabeen Lake near and around the mouth of Deep Creek at about the same time as at Boambee. The trees were all natural regeneration, open grown and mainly small (up to 11 metres high).

The eggs were laid mostly on the dorsal surface (*E. botryoides* also has dorsiventral leaves) and the nymphs all established themselves on the ventral surfaces. The population in this area was kept under observation until 1968. The population numbers were high until September, 1967 but very rapidly diminished. After November 1967 it was difficult to find any of the insects; they are still present but in low numbers.

In November 1973 there was evidence of severe damage on *E. saligna* at Bulli Pass; no eggs or nymphs were seen but the remnant lerps of fully grown nymphs were observed. Damage to the foliage was so severe that probably only a relict population was present.

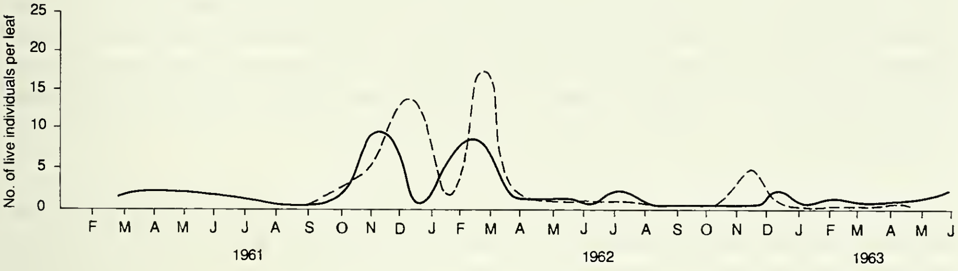

Fig. 6. Population trends of *Cardiaspina fiscella* at Boambee Plantation. Eggs (----), nymphs (____).

DISCUSSION

Sites

All the areas where outbreaks of these psyllids occurred in the 1960-63 period had several characteristics in common. These are listed below.

(i) The trees were at least five years old and therefore producing mature foliage.
(ii) They all grow in 'valley bottom' conditions with abundant soil moisture and nutrients.
(iii) None of the areas had suffered from wildfire or controlled burning since they were established.

Weather

There appears to be a connection between 'wet' years and psyllid outbreaks. In the Boambee area the greater part of the rain usually falls in the summer and a 'dry' year means below average rainfall in this season; 'dry' years were recorded in 1932, 41, 46, 48, 57 and 60. The summers of 1961/2 and 1962/3 were both 'wet' years and cyclonic conditions caused above average rainfall in both these seasons. Some data for recent years are summarized below.

Wet Years: 1942, 43, 44, 45, 47, 49/50, 58/59, 61/62/63
Psyllid Outbreaks Recorded: 1944, 45, 47, 48, 57, 61,62

However, before this apparent correlation can be established many more data are necessary. The direct and indirect effects of weather on insect populations have been discussed by Nicholson (1954) and de Bach (1958). Clark (1962) also discussed the effects of weather-induced breakdowns of the host and parasite synchronization in *C. albitextura*, as well as the reduction of parasite effectiveness in weather conditions unfavourable to them. White (1969) has studied in detail the effects of weather on outbreaks of psyllids and their host trees, particularly *C. densitexta* and *E. fasciculosa* and has evolved a 'stress index' to explain the complex interactions of this important factor.

Life Histories and Behaviour

The concept of one species-one niche appears to be negated by the two distinct species of closely related insects occupying the same host. *C. maniformis* and *C. fiscella* co-exist on the same part of the same host, the dorsiventral leaf of *E. grandis*.

Studies have revealed that although adult females may oviposit on the same leaf surface, after eclosion the nymphs choose quite different feeding sites though often on the same leaves. *C. maniformis* establishes itself on the dorsal surface of a leaf and remains there throughout its nymphal life, whereas *C. fiscella* lives and feeds on the ventral surface, commonly of the same leaf. Interspecific competition is minimized by this difference in feeding site preference. The two species indeed do occupy different niches even though they are otherwise subject to similar habitat conditions. This behaviour does not appear to be unfavourable to either species, as they are able to attain high numbers on the same host at the same site at the same time.

It was notable that *C. maniformis* predominated over *C. fiscella* in the Boambee Plantation where the crowns of the trees are very close together; in this closed canopy situation sunlight would be limiting. In the natural regeneration area, where the crowns were not touching and sunlight was abundant, *C. fiscella* predominated in numbers in the proportion of about 6:1. It appears that lower light intensity is less favourable to *C. fiscella* nymphs. A dorsiventral leaf presents its dorsal surface incident to the light so that a shaded leaf, not so actively photosynthesizing and transpiring less will tend to have more of its stomatal apertures closed than one in full sunlight. This may restrict the nymphal stylets and reduce the food supply to a psyllid feeding on the ventral surface. Of course, the physiological reactions of tree leaves with regard to the ambient humidity, $C0_2$ concentration, sunlight and soil moisture are quite complex and effects of these factors in leaf sap-sucking insects of trees are little known.

There is no doubt that this interaction between nymphal feeding and leaf condition is important both to the tree and the insect. As suggested previously, it is possible for a forest stand (or a single tree) to more or less regulate a psyllid plague in the following way. The adult and nymph both need a sufficient supply of healthy and appropriate leaf tissue, but damage to a leaf to a critical stage will without exception result in shedding of that leaf. If plague numbers are present, damage to a great number of leaves will occur and defoliation of many trees will result.

If sufficient refoliation does not occur (or enough suitable foliage remain), when the surviving adults of the previous generation emerge and require ample oviposition sites, then eggs will be laid on sites which give the nymphs little chance of survival. Too few will reach full growth to maintain high population numbers and consequently the population will decline. Some psyllids will usually survive and other mortality factors may hold them at low levels for some time until another favourable situation occurs to permit another increase in numbers.

The ability of *E. grandis* trees to withstand leaf damage and to refoliate rapidly and successfully depends on their energy reserves built up in periods when they are not under stress (from insect attack or drought). Vegetative growth is considered to be encouraged by a plentiful supply of available nitrogen. The apparent connection between 'wet' years and psyllid outbreak release may be due to the increased availability of atmospheric nitrogen to trees, because of increased thunderstorm activity in such years. In the case of flooded gum, soil moisture and light are not limiting and the ready production of healthy leaves essential for high psyllid numbers is also enhanced by the high levels of available nitrogen.

Other factors affecting the incidence of psyllids are parasites and predators. The primary wasp endoparasites (*P. gemitus* and others) caused considerable mortality of the psyllid nymphs of both species in several generations in 1961-62, though their longer term effect was reduced by the hyperparasitizm by *P. clarus* and *Quaylea psyllae*. Clark (1964a) also discussed the effects of parasites on *C. albitextura* in some detail.

The predatory larvae of the syrphid fly accounted for the deaths of many psyllid nymphs, but more so in the open grown trees of South Boambee, presumably more favourable for the adult flies. The syrphid is an important controlling factor, but in turn is a favourite food of insectivorous birds.

The several insectivorous birds present also accounted for many insects present in the habitat, but these predators were not selecting for particular groups of insect prey. In eating an insect, the bird directly reduces its numbers, but if the parasites or predators of the insect are also eaten a net increase in the insects' numbers may result. The interactions are extremely complex and findings of studies done so far, controversial (Campbell and Moore, 1957; Clark, 1964b; Readshaw, 1964; Ward and Neumann, 1982).

Causes of Psyllid Outbreaks

Drawing together the available information the following hypothesis has been developed to explain the processes that lead to a psyllid outbreak. It is presented here for consideration.

In years when above average summer rainfall occurs, increased thunderstorm activity makes more atmospheric nitrogen available to trees during the growing season; the trees then produce more than adequate high quality foliage. The psyllids, already present in low numbers, are able to take advantage of plentiful and favourable oviposition and nymphal feeding sites and large numbers will survive to adulthood. The biotic mortality factors (endoparasitic wasps, predatory fly larvae, birds), previously maintaining the psyllids at low numbers, cannot now cope with this rapid increase in numbers. Increased numbers of well nourished and vigorous psyllid adults survive and are able to lay many more viable eggs, with many more nymphs surviving to maturity. An exponential increase of the population to plague numbers results.

At this stage the condition of the foliage may become a limiting factor. If damage caused by nymphal feeding is great enough, severe defoliation of the trees will adversely affect survival and reduce numbers of the psyllids. If the biotic mortality factors or overcrowding can limit the psyllid numbers below this level of damage the defoliation may only be partial, giving some respite to the trees so that new leaves can be produced. If the new leaves are produced in time for them to mature and become suitable oviposition sites and feeding sites for the next generation of psyllids, then the population will be maintained at a high level. If not, psyllid numbers must decrease and the biotic mortality factors can again limit psyllid numbers at a lower level. This may continue until another favourable cycle of conditions for outbreak release occurs.

The author considers that the weather, as manifested in below average summer rainfall, is the major 'legislative' factor in maintaining these psyllid populations at low numbers; but it is still not clear whether or not it is the 'governing' factor (Nicholson, 1954).

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